DESCRIPTION AND OSTEOLOGY OF *THRYSSOCYPRIS,* A NEW GENUS OF ANCHOVYLIKE CYPRINID FISHES, BASED ON TWO NEW SPECIES FROM SOUTHEAST ASIA

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ABSTRACT: *Thryssocypris* new genus comprises two new species, the generic type-species *T. smaragdinus* from the Kapuas River in Kalimantan Barat (Indonesian western Borneo) and *T. tonlesapensis* from the lower Mekong basin in Kampuchea and Vietnam. Extremely compressed and anchovylike, *Thryssocypris* differs from all other cyprinids in having a non-protrusible upper jaw with the posterior half of its margin formed solely by the maxilla, and a pair of elongate, slitlike supraethmoidal laterosensory trenches. Osteological study reveals features of the Weberian apparatus, gill arches, pelvic girdle, and terminal radials of the dorsal and anal fins that have not been reported previously in cyprinids. The two new species differ in proportions and fin positions, in numbers of anal fin rays, scales, and vertebrae, and in coloration. The relationships of the new genus to other cyprinids require further study.

INTRODUCTION

Two recently discovered, anchovylike, insectivorous cyprinid fishes, one from the Kapuas River in western Borneo (Kalimantan Barat, Indonesia) and the other from the lower Mekong basin in Kampuchea and Vietnam, are closely related to each other and represent a highly specialized new genus. We do not know of any previously described species referable to this genus.

Five specimens of the Bornean species were obtained at a single locality during an ichthyological survey of the Kapuas River in 1976, and we have been unable to locate any additional material of this species. Nine specimens of the

Mekong species were obtained by F. d'Aubenton during a survey of the Tonle Sap in 1961, and at least one hundred specimens by W. J. Rainboth during a University of Michigan fisheries survey in the Mekong Delta in 1974. This species also does not seem to have been collected previously. The species differ so markedly in head size and other characters that they were not immediately recognized as congeneric. However, closer comparison, including osteological study, revealed that they agree in numerous characters not found, or at least not reported, in any other cyprinids and that they clearly do belong in the same genus.

Cyprinidae is the largest family of freshwater fishes, and we are very far from a phyletic classification of the genera or even a reasonable division of the family into taxonomic categories above the generic level. A great deal of work remains to be done in order to provide adequate definitions for cyprinid genera, many of which, as currently understood, are polyphyletic and must be split up before a phyletic classification can be achieved. Since many distinctive cyprinid genera are relatively rare, and live specimens virtually unobtainable, classification must be based mainly on information that can be extracted from preserved specimens. Osteological accounts of distinctive genera, especially if extensively illustrated in a standardized format (e.g., that of *Brycon* by Weitzman 1962) provide perhaps the most ready source of information for use in phyletic classification. Unfortunately, there is a dearth of such accounts. In addition to describing this new genus and its two species, therefore, we present an account of its osteology.

MATERIAL AND METHODS

Material of the two species described herein is deposited in the following institutions: California Academy of Sciences (CAS), Museum of Zoology of the University of Michigan (UMMZ), Smithsonian Institution (USNM), Museum national d'Histoire naturelle, Paris (MNHN), Museum d'Histoire naturelle de Genève (MHNG), Museum Zoologicum Bogorense, Bogor, Indonesia (MZB). The osteological account is based on a 53.2-mm paratype of *T. smaragdinus* and a 46.0-mm paratype of *T. tonlesapensis,* which were cleared and stained in alcian blue and alizarin. Additional osteological observations were made on radiographs of the other four type specimens of *T. smaragdinus* and 12 of the largest *T. tonlesapensis.* Although our osteological figures are based mainly on *T. smaragdinus,* our remarks generally relate to the osteology of both species. While it is not always so in fishes prepared with alcian and alizarin, in our material of *T. smaragdinus* and *T. tonlesapensis,* except for the distal ends of the intermuscular bones, it seems that all skeletal elements stained with alcian are true cartilage; all stained with alizarin are true bone. In the figures bone is indicated by stipple, cartilage by simple diagonal hatching, and fenestrae or foramina opening into intracra-

nial spaces by cross-hatching. In all of the figures the scale bar equals 1 mm.

We draw attention to a few reservations concerning the osteology. The parietal laterosensory canal bony tubules and supraoccipital crest were badly damaged in the 53.2-mm specimen illustrated and were drawn on the basis of reconstruction and comparison with whole, unstained specimens. The shape of the posteriormost portions of the prevomer and parasphenoid and their relationships to other elements were not observed with certainty in the specimen illustrated and may be in error. In particular, the appearance of the prevomer may be due to breakage rather than to mere separation. We did not detect an intercalar, an element sometimes absent in Cyprinidae, but are uncertain of its absence in the present instance. Otoliths were not removed so that the crania could be preserved intact, and thus they are not described or figured.

Thryssocypris, new genus

TYPE-SPECIES.—*Thryssocypris smaragdinus* Roberts and Kottelat, new species.

DIAGNOSIS.—Small (largest specimen 63.8 mm), anchovylike cyprinids with highly compressed head and body; barbels absent; exceptionally large olfactory organ; well-developed hyaline eyelid; elongate, moderately upturned, and very narrow terminal jaws; acutely pointed snout, slightly to strongly projecting anterior to upper jaw; low dorsal and anal fins, with falcate margins, originating in posterior half of body; abdomen rounded, without keel. *Thryssocypris* differ from all other known cyprinid genera in the following characters: 1) upper jaw entirely nonprotrusible, without rostral cap or even vestigial groove of rostral cap, with posterior half of border formed solely by maxilla; 2) cephalic laterosensory system with elongate, slitlike supraethmoidal or rostral canal medial to nasal canal, supraorbital canals similarly slitlike, not enclosed in bony tubules on frontal bone, and an elongate dermosphenotic canal enclosed in a bony tubule fused for entire length to dorsal surface of sphenotic bone; 3) ventral portion of gill arches highly specialized, ceratobranchials 1–4 with proximal portions abruptly narrowed and ending in elongate cartilaginous extensions, hypobranchial one minute and hypobranchials 2–3

FIGURE 1. *Thryssocypris smaragdinus*, 49.4-mm holotype (MZB 3435).

absent, and basibranchials extremely slender; 4) Weberian apparatus with lateral process of centrum 2 extremely elongate and strongly curved posteriorly dorsal to tripus, extending laterally equally as far as fully formed pleural rib of fifth vertebra; 5) ischiac process of pelvic girdle with elongate and extremely slender anterior and posterior processes; and 6) posteriormost pterygiophore of dorsal and anal fins with a deeply bifurcate radial projecting considerably beyond base of posteriormost fin rays.

Regarding the diagnostic characters listed above: 1) a few other cyprinids have nonprotrusible upper jaws (e.g., the North American *Exoglossum* and *Parexoglossum*), but in these and all other cyprinids known to us the maxilla is entirely or almost entirely excluded from the gape by the premaxilla; 2) some other cyprinids apparently have laterosensory canals in the supraethmoidal region (e.g., *Luciosoma*), but the position and shape of these canals is quite different from those in *Thryssocypris,* and they are not slitlike. Lekander (1949) reported rostral laterosensory organs in some European cyprinids, but these are more anterior (near snout tip) and are joined by a commissure (absent in *Thrys-*

socypris). Supraorbital canals in Cyprinidae are usually enclosed in bony tubules on the dorsal surface of the frontal bone. A dermosphenotic laterosensory canal is present in most cyprinids, but usually occurs in a short segment of bony tubule or on a small laminar dermosphenotic bone that is completely separate and superficial to the sphenotic bone; 3) in all other cyprinids we have examined or know about the gill arches have ceratobranchials 1–4 uniformly wide and hypobranchials one to three present; 4) many cyprinids have a very large lateral process on centrum two, but in most instances it projects directly laterally from the vertebral column, or in some instances is strongly curved posteriorly but projects ventrally to the tripus (rather than dorsally to it as in *Thryssocypris*); 5–6) the unusual condition of the ischiac process and of the terminal radials in the dorsal and anal fins is unlike anything we know of or have seen reported in any other cyprinids.

A more detailed account of the osteology of *Thryssocypris* is given following the species descriptions. Some additional characters of the genus are given here. Lateral line complete, moderately curved downward anteriorly. Gill rakers
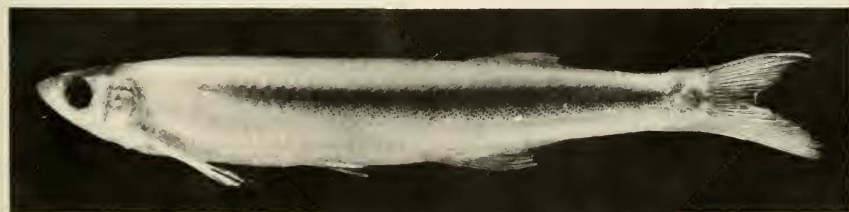

FIGURE 2. *Thryssocypris tonlesapensis*, 50.6-mm holotype (MNHN 1982–1032).

TABLE 1.   QUANTITATIVE CHARACTERS IN *Thryssocypris*.

Character	T. smaragdinus	T. tonlesapensis
Counts		
Gill rakers on first gill arch[1]	0+7	0+8
Pharyngeal teeth (left/right)[1]	1+5/5+1	2+5/5+2
Dorsal fin rays	9½(1),10½(3)	9½(3),10½(9)
Anal fin rays	12½(1),13½(2),14½(1)	15½(12),16½(6)
Pectoral fin rays	11–12	10–12
Pelvic fin rays	7–8	7–8
Procurrent caudal fin rays	9+9	9+8–9
Scales in lateral series	36–39	43–46
Scale rows above + below lateral line	5+3	6+3
Median predorsal scales	25?–27?	26–31
Circumferential scales	18–20	18–21
Circumpeduncular scales	14–15	16–17
Abdominal + caudal = total vertebrae	21+17 = 38(2),21+18 = 39(3)	21+22 = 43(12),21+23 = 44(1)
Proportions (times in standard length)		
Head	3.8–4.1	4.9–5.3
Snout	12.0–12.5	15.4–16.9
Olfactory organ	18.4–22.4	33.6–34.7
Eye	15.5–17.0	19.2–24.8
Lower jaw[1]	7.9	10.7
Pharyngeal bone[1]	11.4	20.0
Body depth	5.1–5.5	6.2–6.8
Body width	9.9–11.1	12.2–14.3
Caudal peduncle depth	11.4–12.0	10.6–11.5
Pectoral fin	5.7–6.1	6.0–7.0
Pelvic fin	9.0–10.0	8.9–9.7
Preanal length	1.3–1.4	1.5–1.6
Other		
Inclination of jaws	25°	30–35°

[1] From cleared and stained specimens.

small, short, and somewhat stubby, leading edge of lower limb of first gill arch with seven to eight rakers, upper limb with none to one. Pharyngeal teeth uncinate, in two rows, 1–2+5/5+2–1. Scales large, 36–46 in lateral series, approximately correlated in number with vertebrae, which total 38–44. Quantitative characters of the genus are summarized in Table 1.

Dorsal and ventral profiles of head and body anterior to dorsal and anal fins uniformly and gently curved (not forming an angle at occiput or pectoral fin origin). Dorsal and ventral surface of body anterior to median fins rounded from side to side. Body moderately tapered caudally (markedly tapered in some cheline cyprinids). No indication of a cranial flexure. Morphological features related to ability of head to tilt upwards in relation to vertebral column (evidently a feeding adaptation in Asian cyprinids such as *Macrochirichthys, Salmostoma, Oxygaster,* and *Che-*

la) are absent. Epaxial musculature does not invade cranial roof, angle of occiput is relatively acute, and parasphenoid relatively horizontal.

Scales on dorsum, sides (including lateral line scale series), caudal peduncle, and abdomen morphologically similar, except that scales of lateral line series have simple tubule for laterosensory canal, horizontally oriented, originating at or near focus and extending for half or more than half length of posterior field. Shape modified oval; anterior, dorsal, and ventral margins slightly convex, posterior margin rounded or even slightly pointed (especially in median scale rows and near bases of paired and median fins), sometimes weakly scalloped. Dorsal and ventral fields more or less sharply set off from anterior field but grading smoothly into posterior field. Radii present on all fields, but best developed on anterior and posterior fields. Radii on anterior field 8–15, horizontally oriented (parallel to each other). Radii

FIGURE 3. *Thryssocypris smaragdinus,* 49.7 mm, twenty-third scale in lateral line scale row (Nomarski interference contrast optics).

on posterior field 22–30 or more, slightly divergent from horizontal, more widely separated than those on anterior field. Radii on anterior and posterior fields originating near focus. Radii on dorsal and ventral fields similar, few in number, widely divergent, and variable in length, originating remote from focus, nearly parallel to uppermost and lowermost radii in posterior field, with which they seem to form a continuous series, and entirely divergent from radii in anterior field. Circuli well defined and evenly spaced in anterior, dorsal, and ventral fields, but discontinued or indistinct on posterior field. Circuli of anterior field vertical, of dorsal and ventral fields horizontal; circuli of dorsal and ventral fields meeting at right angles with circuli of anterior field at interfield margins, and bisecting growth

lines of posterior field at a sharp angle. Growth lines, readily observable in posterior field, much more numerous and more nearly circular in arrangement than circuli.

Multicellular horny projections, or tubercles (also known as breeding tubercles), absent from body and fins, and perhaps also from head. Numerous minute conical projections toward tip of snout, on upper lip, and on lacrimal area of head (especially near ventrolateral margin of infraorbital 1) appear to be tubercles. Tubercles frequently occur on dorsal surface of pectoral fins, on scales, and on mandible in many cyprinids, especially in males, but are absent from these places in *Thryssocypris.*

ETYMOLOGY. — From the Greek *thrissos,* a herring or anchovy, and *cypris,* a small minnow.
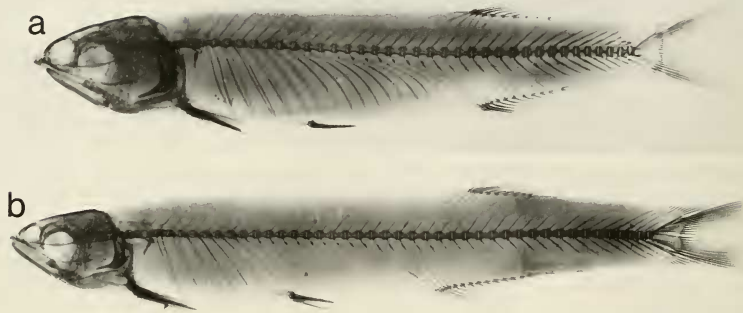
FIGURE 4.   *Thryssocypris*, radiographs. a, *T. smaragdinus*, 49.4 mm (holotype); b, *T. tonlesapensis*, 52.0 mm (paratype, CAS 50946). Note obvious differences between species but also basically identical morphology of skulls.

Thryssocypris smaragdinus, new species

(Figures 1, 3a, 4–9, 10b, 11–19)

HOLOTYPE.—MZB 3435, 49.4 mm, mainstream of upper Kapuas River, 6 km w of Putussibau, Kalimantan Barat, Indonesia, lat. 0°50.5′N, long. 112°52′E. Seining in late afternoon and at dusk, on gently sloping open beach with coarse sand to fine gravel bottom and moderate current. 9 Aug. 1976.

PARATYPES.—CAS 49314, 3: 46.8–54.0 mm, and USNM 230243, 1: 49.7 mm, collected with holotype.

DIAGNOSIS.— *Thryssocypris smaragdinus* is most readily distinguished from *T. tonlesapensis,* its only congener, by much larger head, larger eye, larger pharyngeal bone, and fewer anal fin rays, scales, and vertebrae. These and other quantitative characters differing in the two species are summarized in Table 1. In *T. smaragdinus,* anal fin origin on a vertical with dorsal fin origin (versus anal fin origin far in advance of dorsal fin origin in *T. tonlesapensis*). Snout tip projects strongly beyond upper jaw in four of the five specimens of *T. smaragdinus* (including the holotype), thus differing strikingly from *T. tonlesapensis,* in which it projects but very slightly. In one paratype of *T. smaragdinus* (USNM 230243, 49.7 mm), however, the snout tip projects little more than in *T. tonlesapensis.* Some additional differences between the two species are indicated in the color descriptions below and in the osteological account following.

In life *T. smaragdinus* are brilliant emerald green on the upper half of the head and body and bright silvery below. Preserved specimens exhibit a wide longitudinal band, narrowest an-

teriorly, extending from head to caudal fin, and lying entirely in dorsal half of body. Middle of caudal peduncle and caudal fin base with dark round spot level with longitudinal band. Melanophores absent from all fins except for a few small scattered ones on interradial membranes of dorsal and caudal fins. Melanophores almost entirely absent on ventral half of body. Dorsal half of body with numerous fine melanophores or chromatophores in addition to those of longitudinal band, but not forming noticeable patterns such as rows parallel to posterior margin of scales. Dorsal midline of body with two or three thin longitudinal rows of melanophores. Dorsal surface of head, especially dorsal to nasal organs, deeply pigmented with numerous large melanophores. Inner surface of opercle dusky.

Gut contents of 53.2-mm paratype comprise moderately numerous triturated remains of aquatic coleopteran and dipteran larvae, and some adult winged dipterans. No other food items observed.

ETYMOLOGY.—From the Greek *smaragdinos,* emerald green.

Thryssocypris tonlesapensis, new species

(Figures 2, 3b, 10a)

HOLOTYPE.—MNHN 1982–1032, 50.6 mm, Prek Tamen, at or near Snoc Trou, Kampuchea, 9 Nov. 1961.

PARATYPES.—MNHN 1982–1033, 3: 44.7–50.3 mm, MHNG 2119.63–64, 2: 45.5–46.0 mm, CAS 50946, 2: 48.4–52.1 mm, collected with holotype; MNHN 1982–1034, 1: 52.3 mm, Prek Tasom, at or near Snoc Trou, Kampuchea, June 1961; UMMZ
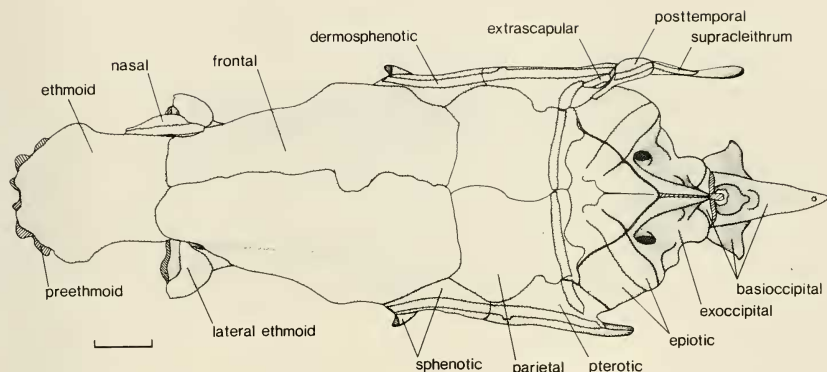
FIGURE 5.   *Thryssocypris smaragdinus,* 53.2 mm, cranium (dorsal view).

210277, 1: 43.4 mm, Mekong River at w end of Con Phong (or Con Ho?) Island 2–5 km w of My Tho, Vietnam, 18 July 1974; UMMZ 210278, 1: 45.7 mm, Mekong River at Con Ho Island, My Tho, Vietnam, 19 June 1974; UMMZ 210279, 58: 20.4–60.1 mm, fish market at Vinh Long, Vietnam, 22 June 1974; UMMZ 210280, 36: 29.2–63.8 mm, fish market at Can Tho, Phong Dinh Province, Vietnam, 23 June 1974.

DIAGNOSIS.—Characters distinguishing *T. tonlesapensis* from *T. smaragdinus* are given in the diagnosis of *T. smaragdinus,* in Table 1, in the description of coloration and other remarks below, and in the osteological account following. The species is immediately distinguished from *T. smaragdinus* by its much smaller head, more numerous scales (44–46 in lateral line series versus 36–39), and more numerous anal fin rays (15½–16½ versus 12½–14½). The very striking difference in size of the pharyngeal jaws of *tonlesapensis* (Fig. 4), the linear dimensions of which are only about half as great as in *T. smaragdinus,* is much greater than would be expected if this difference were due only to the difference in head size, since the head is only about 20% longer in *T. smaragdinus.*

Coloration of live *T. tonlesapensis* has not been observed. Specimens observed in fish markets by W. J. Rainboth were entirely silvery. Color pattern of preserved specimens is similar in its basic features to that of *T. smaragdinus,* including the longitudinal band and basicaudal spot, but differing in some details: longitudinal band lower, nearly midlateral in position (confined to dorsal half of body in *T. smaragdinus*); mela-

nophores on dorsal half of body tending to form rows parallel to posterior margins of scales; and inside of opercle clear instead of dusky.

Guts of numerous specimens are moderately to very full of insects, mostly aquatic larvae; no other food items observed.

ETYMOLOGY.—From Tonle Sap, the enormous permanent backwater of the lower Mekong, into which the Prek Tamen and Prek Tasom flow.

OSTEOLOGY

Although the two species of *Thryssocypris* differ strikingly in skull size and there are obvious differences in the axial skeleton and median fin skeletons related to differences in vertebral number and anal fin position and ray number, their osteology is very similar in most respects (Fig. 4). Some osteological differences between the two species are noted in the following account, which is based on both species, even though the drawings (except Fig. 10a) are of *T. smaragdinus.*

CRANIUM (Figs. 5–8, 10).—Roof of cranium entire, without fontanel, strongly convex transversely for its entire length. Frontals with narrow, flangelike, nearly horizontal lateral margins, and a transverse shallow depression or groove overlying tectum cranii or epiphyseal bar. Sphenotic as well as pterotic bones contribute substantially to cranial roof, with moderately developed sphenotic and pterotic projections or spines. Ethmoid (or supraethmoid) very large,
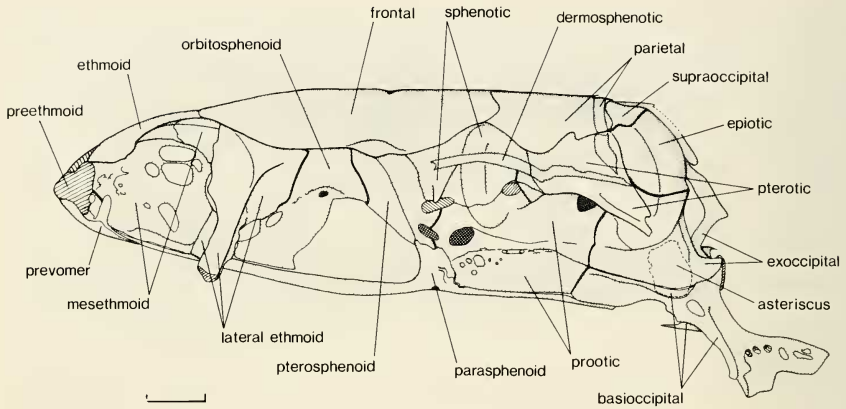
FIGURE 6.   *Thryssocypris smaragdinus,* 53.2 mm, cranium (lateral view).

completely covering mesethmoid so that it does not contribute to dorsal surface of ethmoid region. Preethmoids cartilaginous. Dilatator fossae indistinct. Posttemporal fossae absent.

In most cyprinids the cranium tends to be dorsally flattened, or even transversely concave. In rasborines and bariliines the cranium tends to be barrel-shaped (Gosline 1975), with a convex dorsum, as in *Thryssocypris.* The sphenotic is usually entirely or almost entirely excluded from the dorsal roof of the cranium, a noted exception occurring in *Esomus* (Ramaswami 1955), which in other respects differs very much from *Thryssocypris.* In Cyprinidae the ethmoid is usually much shorter than in *Thryssocypris,* broader than long, and with its anterior margin broadly and deeply indented medially to receive the kinethmoid (*Thryssocypris* has only a very small indentation anteriorly; see Fig. 5).
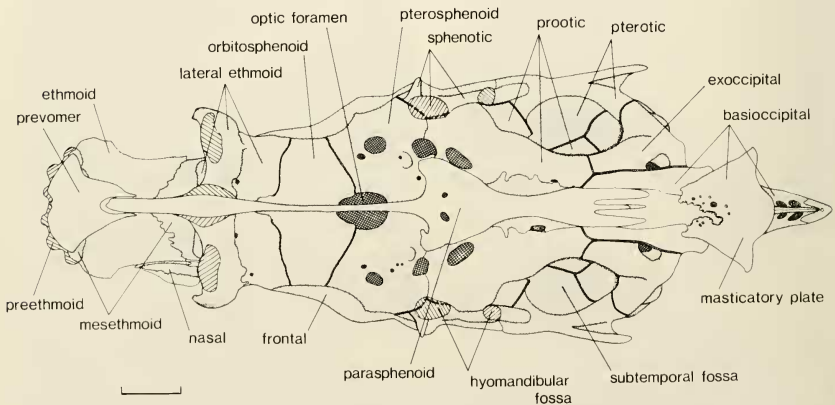
In chelines (Howes 1979) the cranium is more

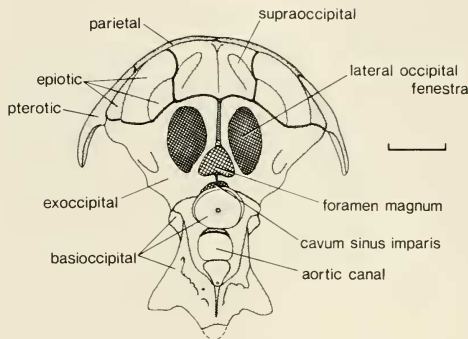FIGURE 7.   *Thryssocypris smaragdinus,* 53.2 mm, cranium (ventral view).

FIGURE 8. *Thryssocypris smaragdinus,* 53.2 mm, cranium (occipital view).

or less flat or even concave dorsally, the mes-ethmoid forms a shelflike projection extending anteriorly to the ethmoid, the anterior half of the parasphenoid is oriented at an angle of about 20° to 30° from the horizontal, the supraoccipital crest tends to be dorsal in position, and the occiput is elongated and gently sloping. In all of these respects chelines differ from *Thryssocypris.*

JAWS (Figs. 9–11).—Jaws elongate, upturned, and very narrow. Premaxilla only half as long as maxilla, maxilla alone forming margin of posterior half of upper jaw (maxilla entirely excluded or almost entirely excluded from gape in all other cyprinids). In *T. smaragdinus* maxilla with two ascending or ethmoid processes, each with a cartilaginous cap, anterior process moderately elongate or pedicellate, posterior process short (Fig. 11); in *T. tonlesapensis* maxilla with only a single
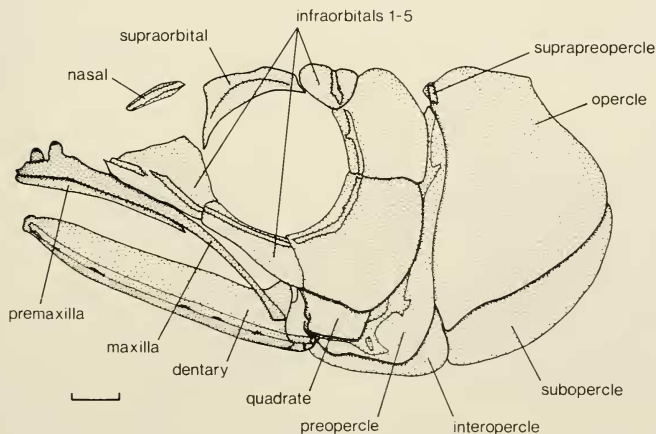

FIGURE 9. *Thryssocypris smaragdinus,* 53.2 mm, jaws and facial bones (lateral view).
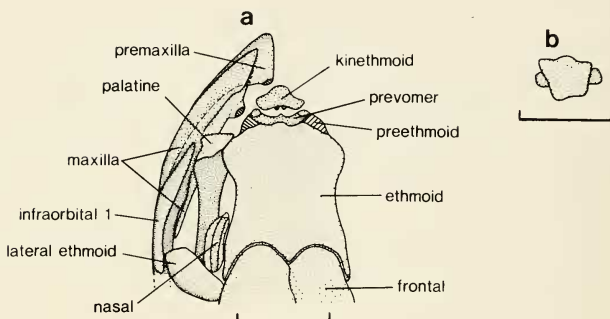
FIGURE 10. a, *Thryssocypris tonlesapensis,* 46.0 mm, ethmoid region of skull (dorsal view); b, *Thryssocypris smaragdinus,* 53.2 mm, kinethmoid bone (dorsal view).

ethmoid process, short and broad based (non-pedicellate), and with a cartilaginous cap (Fig. 10). Anterior half of maxilla with a medially directed shelf arising from its dorsal margin, coextensive with and largely overlapping lateral surface of premaxilla. Maxilla with a slender, posteriorly curved, broad-based projection arising near middle of its dorsal surface and extending medially to infraorbital number one, to which it is firmly attached by connective tissue, thus contributing to immobilization of upper jaw. Only posterior half of maxilla free from snout and capable of limited movement. Posterior portion of maxilla, separated from infraorbitals by a shallow groove, simple, elongate, and flexible; ex-

tends to proximal end of dentary. Lower jaw slightly shorter than upper jaw, elongate and very narrow, completely included within gape when mouth is closed. Symphysis of lower jaw without pronounced dorsal or ventral knobs, although vestigial or rudimentary dorsal symphyseal knob may be present, especially in *T. tonlesapensis.* Dorsal margin of dentary with a slight elevation just behind symphysis in *T. tonlesapensis;* in *T. smaragdinus* elevation absent or barely noticeable. Dentary and angular with coronoid processes short, vertically oriented, and separate, that of dentary arising very near proximal end (coronoid process of dentary frequently very large, usually arising near middle of dentary, and not
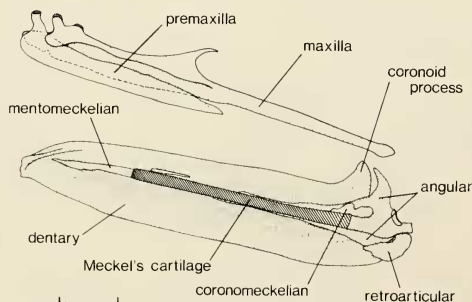

FIGURE 11. *Thryssocypris smaragdinus,* 53.2 mm, jaws (medial view).
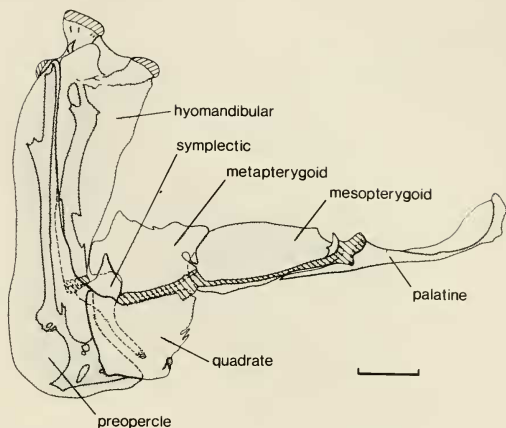
FIGURE 12.   *Thryssocypris smaragdinus,* 53.2 mm, suspensorium (lateral view).

separate from angular in most cyprinids; angular without distinct coronoid process in most cyprinids). Free ventromedian margins of dentary nearly straight for entire length, those of opposite sides in contact or closely approximated (ventromedian margin of dentary frequently highly modified in shape in cyprinids, as in *Danio* and its relatives, and dentaries of opposite sides usually more or less widely separated in cyprinids, including genera with comparably elongate and narrow lower jaws such as *Macrochirichthys, Salmostoma,* and *Securicula*).

The poorly developed condition of the single ethmoid process on the maxilla of *T. tonlesapensis* is suggestive of the condition in chelines, but because the jaws of *Thryssocypris* are otherwise very unlike those of chelines and because *T. smaragdinus* has well-developed ethmoid processes, this resemblance is probably due to independent reduction (possibly related to small size of the head as well as nonprotrusibility of the jaws).

Development of large dorsal symphyseal knobs on each dentary (and sometimes almost equally prominent ventral symphyseal knobs) is characteristic of most chelines, and small dorsal symphyseal knobs occur in many cyprinids, including *Rasbora* and *Barilius*. In forms with dorsal symphyseal knobs the symphysis of the upper jaw is frequently indented for their reception;

there is no comparable indentation in the upper jaw of *Thryssocypris*.

INFRAORBITAL AND NASAL BONES (Fig. 9).— Infraorbital series complete, with five large, lamellar infraorbital bones each bearing a simple bony tubule for infraorbital laterosensory canal and, together with supraorbital bone, forming an almost complete ring around eye. Posterior border of supraorbital indented where concave anterior margin of infraorbital 5 fits snugly against it; slender, pointed, anteroventral projection of supraorbital nearly contacts dorsal margin of infraorbital 1. Nasal bone moderately elongate, with a narrow lamellar portion on either side of bony tubule for nasal laterosensory canal.

Among Asian minnows with elongate, upturned jaws and compressed bodies, a complete infraorbital series in which all five infraorbitals have well-developed lamina is typical of rasborines and bariliines and unusual in chelines (Gosline 1975). In Cyprinidae the primitive number of infraorbitals, exclusive of the dermosphenotic (sometimes counted as an infraorbital), is five. Occasionally a greater number occurs, but this is usually (perhaps invariably) due to fragmentation of more or less tubular infraorbitals in which the lamellar component is greatly reduced or absent.

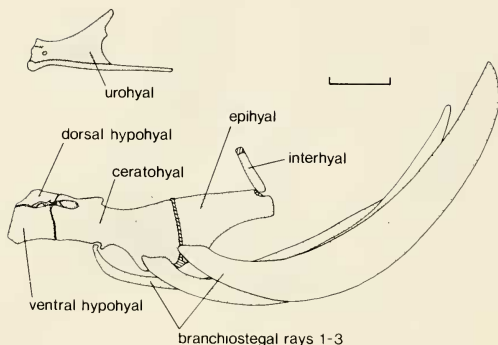SUSPENSORIUM (Fig. 12).—Palatine arch nearly horizontal. Hyomandibular and preopercle ver-

FIGURE 13. *Thryssocypris smaragdinus,* 53.2 mm, hyoid bar and urohyal (lateral view).

tical. Lateral abductor process of hyomandibular dorsally directed, originating just below hyomandibular articulation with cranium. Metapterygoid-quadrate fenestra absent or greatly reduced and almost entirely occluded by peculiarly expanded distal end of symplectic. Anteroventral limb of preopercle extremely short. Quadrate nearly square, with strong posteroventral extension seen in many or most cyprinids, and without a foramen immediately posterior to articular facet for lower jaw. Ectopterygoid apparently absent in *T. smaragdinus*; present but reduced in *T. tonlesapensis.* Palatine bone with a well-developed posteroventral extension underlying lateral ethmoid articular facet. An elongate, continuous palatine cartilage connects palatine bone to mesopterygoid anteriorly and to metapterygoid and quadrate posteriorly. At its anterior end, between palatine bone and mesopterygoid, this cartilage forms a large, saddlelike facet articulating with ventral surface of lateral ethmoid. Opercle generalized in shape, deeper than long, its posterior margin rounded, dilatator process weakly developed. Suprapreopercle short, tubular, fused to anterodorsal corner of opercle.

In chelines the palatine bar is usually upturned like the strongly upturned jaws, and is thus obliquely oriented. Many cyprinids, including some chelines and bariliines, have a well-developed metapterygoid-quadrate fenestra, and most have the quadrate with a well-developed posteroventral process, a preopercle with a prominent anteroventral portion, and a large, broad

ectopterygoid. In *T. smaragdinus* the elongate ventral portion of the mesopterygoid extends narrowly below the palatine cartilage where the ectopterygoid normally occurs, but examination with direct and transmitted light failed to reveal an ectopterygoid. In *T. tonlesapensis* the mesopterygoid does not extend ventral to the palatine cartilage, and a very thin, elongate ectopterygoid is present. Most chelines (Howes 1979) and *Luciobrama* (Howes 1978) have a foramen in the quadrate immediately posterior to its articulation with the lower jaw. Chelines and some other cyprinids tend to have a stout, fingerlike dilatator process forming the elevated anterodorsal corner of the opercle. Some cyprinids have a free suprapreopercle and some lack this element altogether. Fusion of the suprapreopercle with the opercle occurs frequently but is known only in the Cyprinidae. The cyprinid suprapreopercle is always a simple bony tube enclosing the uppermost portion of the preopercular laterosensory canal, never with a laminar portion (sometimes greatly enlarged) as in characoids.

HYOID BAR AND UROHYAL (Fig. 13).—Hyoid bar generalized for Cyprinidae, with three branchiostegal rays as in all members of the family, and no unusual features. First branchiostegal ray articulated to ventral surface of ceratohyal, which has a notch in margin at point of articulation; second branchiostegal ray broadly articulated to lateral face of ceratohyal; third broadly articulated to lateral face of epihyal. Basihyal dorsoventrally compressed, its anterior third cartila-
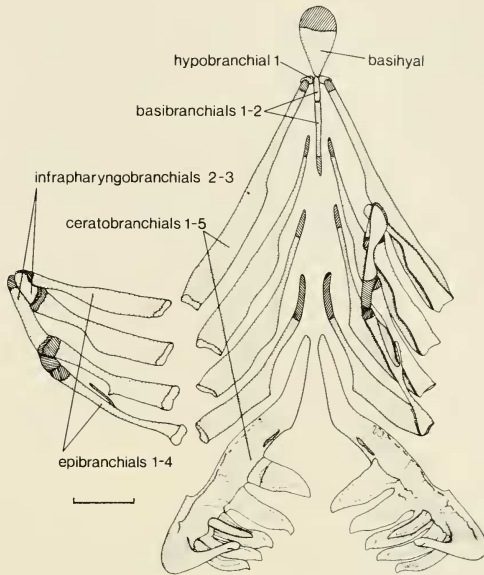
FIGURE 14. *Thryssocypris smaragdinus*, 53.2 mm, gill arches and pharyngeal jaws (dorsal view, with upper half of arches on left side deflected to reveal ventral surface).

ginous and with a broadly rounded anterior margin (basihyal elongate and narrow for its entire length in at least some chelines). Interhyal tubular and moderately elongate (flattened and laterally expanded in some chelines and cultrines). Urohyal with posteroventral process not greatly expanded, its distal end simple in *T. smaragdinus* and with a very small notch in *T. tonlesapensis*. (Urohyal greatly modified in some bottom dwelling cyprinoids including cyprinids; posteroventral process very deeply forked in *Luciobrama* and at least some chelines.)

GILL ARCHES AND PHARYNGEAL JAWS (Fig. 14).—Gill arches (main features described above under generic diagnosis) basically similar in *T. smaragdinus* and *T tonlesapensis*. Narrow proximal portion of ceratobranchials not quite so long as in *T. smaragdinus*, but equally strongly narrowed and with peculiar cartilaginous proximal ends as large as in *T. smaragdinus*. Basibranchials two in *T. smaragdinus*, three in *T. ton-*

lesapensis, extremely slender in both species. Ceratobranchial 5 (tooth-bearing pharyngeal bone) uniformly slender, its length more than five times its width, gracefully arched. External ala elongate but extremely narrow, its origin marked by a small, strongly angular projection opposite base of middle tooth in major tooth row. Ventral edentulous limb slightly shorter, and dorsal edentulous limb slightly longer, than dentigerous portion. Symphyseal half of ventral edentulous limb abruptly narrowed and set at angle to rest of bone, so its orientation is nearly horizontal. Pharyngeal teeth uncinate (conical with recurved tips), in two rows; those of inner or major row uniformly decreasing in size from front to back, those of minor or outer row substantially smaller than those of major row.

Like most cyprinids *Thryssocypris* has but two infrapharyngobranchials, here interpreted as infrapharyngobranchials 2–3. They exhibit the characteristic two-plus-two relationship with
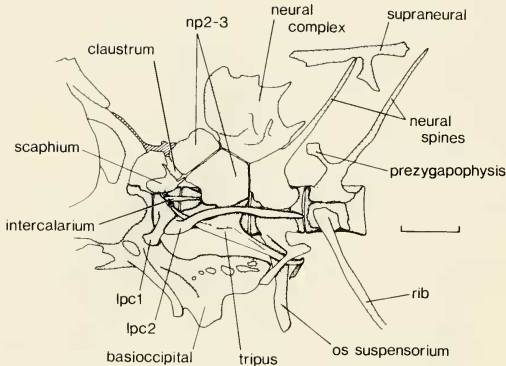
FIGURE 15.   *Thryssocypris smaragdinus,* 53.2 mm, Weberian apparatus (lateral view) (1pc1,2 = lateral processes of centrum 1 and centrum 2; np2,3 = neural plates of centrum 2 and centrum 3).

epibranchials 1–2 and 3–4 which seems to be characteristic of all cyprinoids. Epibranchials 1–2 are united by cartilaginous joints to the distal end of infrapharyngobranchial 2, and epibranchials 3–4 are similarly joined to infrapharyngobranchial 3. Thus the proximal ends of infrapharyngobranchials 1 and 2 approximate each other, and there is a slight but distinct gap between epibranchials 1–2 and epibranchials 3–4. This peculiar orientation, which seems not to have been noted previously, has been observed without exception in numerous cyprinoids examined by us. Although the orientation is highly specialized compared to the primitive one-to-one relationship between the infrapharyngobranchials and epibranchials observed in characoids and most lower teleosts, it is apparently primitive for cyprinoids. A curiously similar two-plus-two arrangement is present in numerous siluroids examined, including *Diplomystes,* but the relationships of the infrapharyngobranchials to the epibranchials appears not to be exactly the same. Further investigation should be done to determine whether this condition in cyprinoids and siluroids indicates a common ancestor for these two groups. In any event this specialized condition is too widespread among cyprinids to be of any use in assessing phyletic relationships of *Thryssocypris.*

In some cyprinoids (mainly bottom feeders,

such as *Labeo* and *Osteochilus,* with inferior, suctorial mouths) the basibranchial bones appear to be shaped and articulated in such a fashion as to permit them to slide over and under each other, thus indicating that the ventral half of the branchial basket is capable of anteroposterior contraction and expansion. In *Thryssocypris* the elongate, slender, and straight basibranchial bones are firmly joined end to end, indicating that the branchial basket is incapable of such contraction and expansion movements.

WEBERIAN APPARATUS (Fig. 15). — Similar generally to Weberian apparatus of *Opsariichthys* (Fink and Fink 1981; Fig. 14). Neural complex vertical (not strongly posteriorly sloped as in many chelines and cultrines), widely separated from occiput. Occiput attached to anterodorsal surface of Weberian apparatus by a thin median strip of cartilage extending from posterodorsal median margins of exoccipitals to claustrum and neural process of centrum number two. Lateral process of centrum 2 exceptionally elongate and strongly curved posteriorly, extending dorsally to tripus and laterally as far as major curvature of fully formed pleural rib of vertebra 5. Fourth pleural rib and parapophysis (bearing os suspensorium) without a prominent anterodorsally projecting lateral process (present in *Opsariichthys*). Intercalarium simple, slender, and elongate, horizontally oriented, without ascending or articular
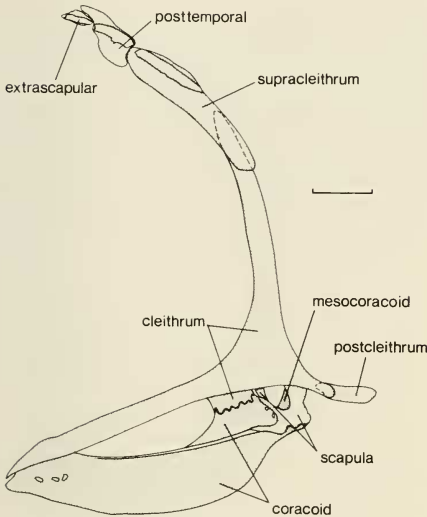
FIGURE 16.   *Thryssocypris smaragdinus*, 53.2 mm, pectoral girdle, left half (lateral view).

processes. Centra 2 and 3 fused to each other, at least ventrally (centra 2–3 separate in *Opsariichthys* but partially or completely fused in many cyprinids).

Endochondral union of Weberian apparatus with cranium is characteristic of cyprinoids and is not found in other ostariophysans (Fink and Fink 1981). Reduction and loss of ascending and articular processes of intercalarium in other ostariophysans, especially siluroids, is reported by Fink and Fink (1981:328). In *Opsariichthys* relatively large gaps occur between neural arches 2–3 and the vertebral column, and between neural arches 3 and 4; these gaps are greatly reduced in *Thryssocypris* (that between neural arches 3 and 4 is completely occluded). The element here termed neural arch of centrum 2 is the anteriormost supraneural according to Fink and Fink (1981).

Fusion of centra 2 and 3 is possibly a primitive character for all Cyprinidae. We propose a hypothesis that this condition evolved only once and that the mosaic distribution of cyprinid gen-

era with fused and with separate centra 2–3 is due to repeated secondary failure to fuse and reversion to the fused condition, rather than to truly independent evolution of fusion between these centra in phyletically diverse lines (the hypothesis seemingly favored by Greenwood et al. [1966:385] and Fink and Fink [1981:331]). Centra 2–3 are fused in the primitive siluroid *Diplomystes*, centra 2–4 and sometimes also 5 in all other siluroids (Hassur 1970). Whether fusion of centra 2–3 evolved independently in siluroids or indicates their phyletic relationship to cyprinoids has not been resolved satisfactorily (compare Roberts 1973 with Fink and Fink 1981). The centra of the Weberian apparatus are all separate in all characoids, gymnotoids, and gonorynchs. In any event this character is unlikely to be relevant in considerations of the closer phyletic relationships of *Thryssocypris*.

PECTORAL GIRDLE (Fig. 16).—Pectoral girdle morphologically generalized, slender, with a single extrascapular (two extrascapulars in some cyprinids), dorsal and anteroventral limbs of cleithrum slender, postcleithrum moderately elongate (slightly more elongate in *T. tonlesapensis* than in *T. smaragdinus*). Coracoid with a strongly developed lateral shelf, but not ventrally expanded; coracoid foramen broad. (Coracoid is ventrally expanded, sometimes enormously so, in most chelines and cultrines. In some, coracoid foramen reduced or even occluded.) In chelines (Howes 1979), postcleithrum frequently (always?) arclike, very slender and elongate, and with distal end projecting downwards, quite unlike the postcleithrum in *Thryssocypris*. In *Thryssocypris* the pectoral fin, although slightly larger proportionately in *T. tonlesapensis* than in *T. smaragdinus*, is not notably enlarged, nor is the simple outer ray thickened or otherwise modified. The pectoral axial flap (attached to the postcleithrum) is simple, moderately elongate, and not overlain by peculiarly shaped scales. In all of these respects the pectoral fin of chelines and cultrines tends to be modified.

PELVIC GIRDLE (Fig. 17).—Pubic bone deeply bifurcate anteriorly (as in most cyprinoids); lateral pubic projection nearly twice as long as medial. Ischiac process highly modified, with extremely elongate anterior and posterior projections. In *T. smaragdinus* anterior ischiac projection about half as long as posterior projection; in *T. tonlesapensis* anterior projection
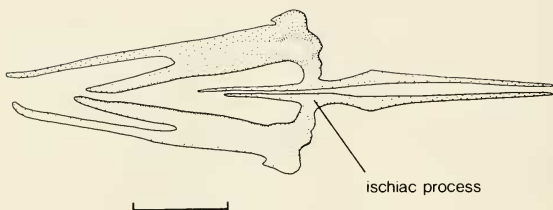
FIGURE 17.   *Thryssocypris smaragdinus,* 53.2 mm, pelvic girdle (ventral view).

twice as long as posterior one, extending ante-
riorly as far as distal end of medial pubic pro-
jection. Origin of ischiac process opposite distal
end of pleural rib of vertebra number 9 in *T.
smaragdinus,* and of pleural rib of vertebra 11
or 12 in *T. tonlesapensis.*

AXIAL SKELETON.—Supraneurals 4–6 in num-
ber, commencing immediately posterior to neur-
al complex of Weberian apparatus (not greatly
enlarged or articulated to each other as in some
chelines). In *T. smaragdinus* vertebrae 5–20 and
in *T. tonlesapensis* 5–16 with enlarged prezyga-
pophyses. *Thryssocypris smaragdinus* with well-
developed dorsal ribs attached to anterior half
of centrum on vertebrae 11–24; *T. tonlesapensis*
without dorsal ribs (dorsal ribs unreported in any
Cyprinidae until now). Pleural ribs of vertebrae
5–10 with broad, laminar proximal ends at-
tached to comparably broad parapophyses; re-
maining pleural ribs with proximal ends slender,

weakly attached to slender parapophyses. In *T.
smaragdinus* proximal portion of pleural ribs on
vertebrae 6–7 with spurlike, posteriorly directed
projections (absent in *T. tonlesapensis*).

The counts of abdominal, caudal, and total
vertebrae in *Thryssocypris* (Table 1) are close or
identical to counts reported in several species of
Barilius by Howes (1980: table 1).

DORSAL AND ANAL FINS (Fig. 18).—Dorsal and
anal fin rays uniformly slender, nonserrate, first
two dorsal and first three anal fin rays simple.
Last complete pterygiophore bears two (counted
as one and a half) fully formed, branched rays;
bases of ray halves of anterior of these two rays
overlap and lie externally to ray halves of pos-
terior ray.

In the anal fin the bifurcate terminal radial (see
generic diagnosis) is the medial radial of the last
pterygiophore, which is complete. In the dorsal
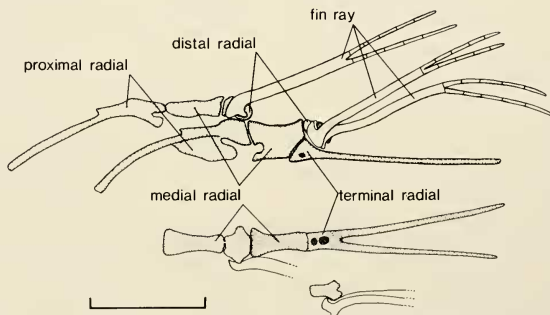fin the situation is more complicated, and the

FIGURE 18.   *Thryssocypris smaragdinus,* 53.2 mm, posteriormost fin rays and pterygiophores in dorsal fin (lateral view above,
dorsal view below).

homology of the bifurcate terminal radial with the proximal, medial, and distal radials is unclear. In *T. smaragdinus* the bifurcate terminal radial constitutes by itself the terminal pterygiophore, articulating endochondrally only with the medial radial of the preceding pterygiophore. In *T. tonlesapensis* an additional element is present ventral to the bifurcate terminal radial; the dorsal margin of this element articulates with the ventral margins of the bifurcate terminal radial and of the preceding medial and proximal radials, and its homology also is unclear.

INTERMUSCULAR BONES.—Intermuscular bones well-developed, epineurals extending entire length of body, epipleurals commencing at vertebra 12. Proximal ends of anteriormost two or three epineurals attached to exoccipital in a small depression or fossa (shown in Fig. 8) near its posterolateral margin and on a level with foramen magnum. Distal ends of posteriormost two or three epineurals and epipleurals multifid (mostly bifid or trifid). Epineurals and epipleurals forked anteriorly with expanded laminae posteriorly.

In chelines and cultrines the anteriormost epineurals tend to insert much higher on the cranium (Howes 1979) than in *Thryssocypris*.

CAUDAL SKELETON (Fig. 19).—Generalized in nearly all respects, with a single epural; one or two uroneurals; parhypural fused to ural centrum, with an exceptionally large, elongate hypurapophysis; six hypurals, separate from each other, with hypurals 1–2 fused to ural complex centrum.

In most lower teleosts with the primitive principal caudal fin ray formula of $10+9$, including all characoids and all Cyprinidae, the caudal fin skeleton tends to be highly conservative, retaining a relatively generalized or primitive morphology, including the primitive complement of six hypurals (exclusive of the parhypural). There is a maximum of three epurals, and perhaps invariably at least one epural. Presumably three is the primitive number of epurals in teleosts including ostariophysans, but reductions to two and one and subsequent reversion to three seem to have occurred repeatedly, particularly often in ostariophysans including Cyprinidae. Thus the single epural in *Thryssocypris* is not likely to be helpful in assessing its relationships to other cyprinids.

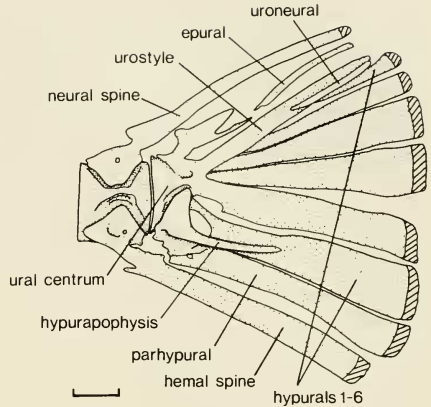It should be noted that previous works on os-

FIGURE 19. *Thryssocypris smaragdinus*, 53.2 mm. caudal fin skeleton (lateral view).

tariophysan caudal skeletons report seven hypurals (e.g., Weitzman 1962; Roberts 1969). Following Monod (1968) the element previously considered as hypural one is here termed the parhypural. The parhypural bears the hypurapophysis which serves as origin of the main muscles for adduction of the upper caudal fin lobe. Thus the hypurals formerly numbered 2–7 are now hypurals 1–6. This new nomenclature has been used by most authors dealing with ostariophysan caudal skeletons subsequent to Monod (1968) including Lundberg and Baskin (1969) and Fink and Fink (1981).

CONCLUSION

The discovery of *Thryssocypris* provides another example of the extraordinary diversity of Cyprinidae, especially in Southeast Asia, and of the close biogeographic relationship between the Kapuas and Mekong basins.

Upon first examining *Thryssocypris* we thought that it might be a specialized *Barilius* or at least closely related to that genus. Lacking osteological information on most other cyprinid genera we are not prepared to discuss its relationships at this time except to note that it does not seem to be related to the chelines (sensu Howes 1979). The specialized characters in *Thryssocypris* that seem most unusual or highly derived and there-

fore likely to indicate phyletic relationships have not been reported in any other cyprinids. These include the peculiar morphology of ceratobranchials and absence of hypobranchials 2–3, shape of jaw bones, elongate anterior and posterior projections of ischiac process, and bifid terminal radials in median fins.

ACKNOWLEDGMENTS

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